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*Trillium channellii*, sp. nov. (Trilliaceae), in Japan, and  
*T. camschatcense* Ker Gawler, Correct Name for the  
Asiatic Diploid *Trillium*

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**ABSTRACT.** *Trillium channellii* (Trilliaceae), a new tetraploid species from eastern Hokkaido (northern Japan), is described. Evidence concerning its relationships with other *Trillium* taxa in Asia is presented and discussed, and hypotheses about its origin are considered. The name *T. camschatcense* Ker Gawler is presented as the correct name for the only diploid *Trillium* species in Asia, a taxon most commonly treated as *T. camtschaticum* Pallas ex Pursh; the latter name was not only published invalidly but also at a later date than the former.

***Trillium channellii*** I. Fukuda, J. D. Freeman & M. Itou, sp. nov. TYPE: Japan. Hokkaido: Kushiro Dist., Kawakami Co., Kawayu area, NW of Teshikaga, 2 km due W of Mt. Yuo, elev. ca. 260 m, rich deciduous forest of *Acer*, *Betula* and *Alnus* on plains near lakeside of Kusharo Lake, 21 May 1994, *Fukuda & Itou s.n.* (holotype, MAK; isotypes, GH, KYO, MO, NY, SAPS, TI, TNS, US, VDB). Figure 1.

A *T. camschatcensi* et *T. tschonoskii* ambobus, quibus facie generali proxime accedit, foliis latioribus, sepalis latioribus et petalis latioribus differt; et a *T. hageae*, cui primo aspectu simillimum est, numero chromosomatum tetraploideorum bene distinctum.

Rhizomatous herb. Aerial stems erect, 30–50 cm tall, glabrous. Leaves 9–12 cm long, 7–14 cm wide, sessile, broadly elliptic, short acuminate at apex, very widely obtuse at base. Pedicels 1.8–2.2 cm long, straight, erect above the leaves. Flowers relatively small, ringent,  $\pm$  perpendicular to the pedicel or slightly angled upward. Sepals lanceolate, 19–44 mm long, 9–18 mm wide, green. Petals ovate, 22–44 mm long, 11–27 mm wide, white. Stamens erect, the anthers 8–10 mm long, the fila-

ments 4–5 mm long. Pistil 10–20 mm long, 7–19 mm wide, the ovary conical, white below and dark purple at apex below bases of purplish stigmatic branches, the stigmas three, spreading, yellowish above. Fruits ovoid to globose, green, with stigmas persistent. Ovules about 226 per pistil. Pollen globose, about 18.6  $\mu$ m diam. Chromosome number:  $2n (4x) = 20$ . See Table 1.

The genus *Trillium* is abundantly represented in Hokkaido, the northernmost main island in Japan. One diploid species and two other tetraploid species besides *T. channellii* occur there as well as hybrids among these taxa at certain locations. Two hexaploid taxa that undergo meiosis and reproduce sexually are assumed to have arisen, either in the distant past or more recently, by somatic doubling of sterile triploid hybrids. The nomenclature of one of the putative parents of the new species named and described herein is clarified later in this article.

The epithet *channellii* was chosen to honor Robert B. (Ben) Channell, Emeritus Professor of Botany, Vanderbilt University, Nashville, Tennessee, U.S.A. His interest in *Trillium* and support of research on taxonomy, cytogenetics, chemistry, and ecology of this genus during the early 1960s account (directly or indirectly) for much new information published about these plants since that time by us as well as many others. He challenged and encouraged those with whom he worked, often without receiving due credit for original ideas. His role in promoting the study of *Trillium* and related genera was acknowledged by Samejima and Samejima (1987), and we add our appreciation to theirs in naming *T. channellii*.



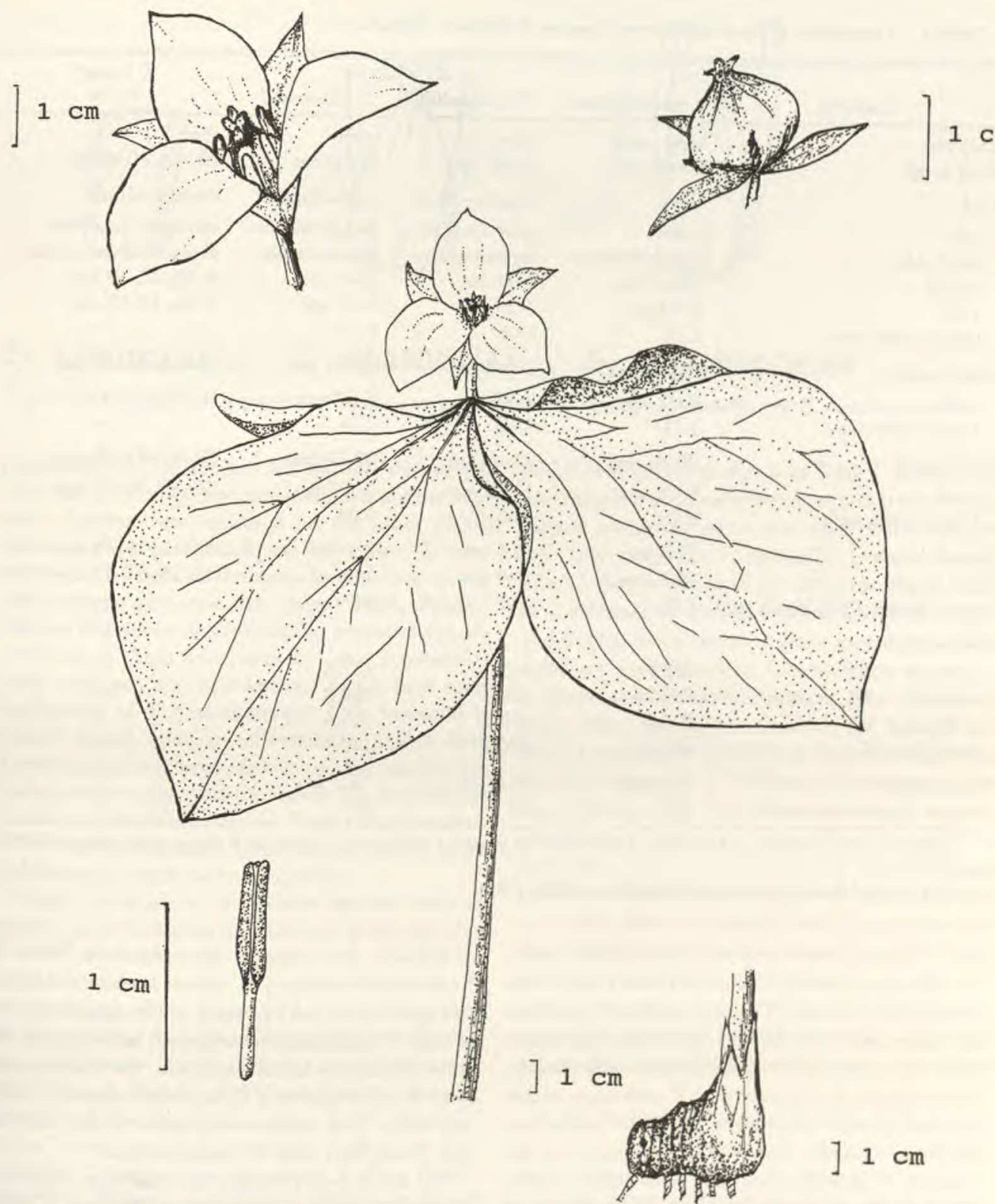


Figure 1. Habit sketch of *Trillium channellii* I. Fukuda, J. D. Freeman & M. Itou, sp. nov. (composite drawing based on the 10 pressed specimens of the type collection, *Fukuda & Itou s.n.*, habit and close-up photographs of plants and flowers taken on 21 May 1994, and photos of fruits taken on 25 July 1994).

THE CORRECT NAME FOR *TRILLIUM CAMSCHATCENSE*

Characters of *Trillium channellii* are compared with those of *T. camschatcense* and *T. tschonoskii* Maximowicz, with which it normally occurs, and *T. hagai* Miyabe & Tatewaki, the only other white-flowered species of *Trillium* in Japan, in Table 1. Before relationships among these taxa can be dis-

cussed in detail, a matter concerning the nomenclature of the only diploid species within the group, a taxon that is closely similar to (if not itself) the contributor of at least one genome in three of the Asiatic polyploids, must be rectified.

The earliest validly published name for the only known diploid *Trillium* species in Asia appears to



Table 1. Comparison of the white-flowered species of Japanese *Trillium*.

Character	<i>T. camschatcense</i> <sup>1</sup>	<i>T. channellii</i> <sup>1</sup>	<i>T. tschonoskii</i> <sup>1</sup>	<i>T. hagai</i> <sup>2</sup> 3x; 6x
Rhizomes	short, stout	same	same	same
Plant height	30–50 cm	30–50 cm	30–50 cm	22–49; 21–46 cm
Leaf	ovate	broadly elliptic	ovate-elliptic	rhombic-elliptic
apex	acute	short acuminate	long acuminate	subacute; cuspidate
basal sides	rounded/convex	obtuse/concave	obtuse/straight	obtuse/straight concave
length	10–17 cm	9–12 cm	10–15 cm	9–18; 12–19 cm
width	7–14 cm	7–14 cm	7–17 cm	9–24; 12–19 cm
length: width ratio	1.19	1.04	1.17	—
Sepal length	26–40 mm	19–44 mm	18–27 mm	23–45; 24–40 mm
width	8–12 mm	9–18 mm	8–12 mm	8–19; 9–16 mm
length: width ratio	3.11	2.48	2.74	—
Petal length	22–47 mm	22–44 mm	22–28 mm	27–49; 27–48 mm
width	9–22 mm	11–27 mm	9–13 mm	16–32; 16–27 mm
length: width ratio	2.15	1.58	2.08	—
Stamen length	17.3 mm	12.8 mm	8.9 mm	12–17; 11–15 mm
Pistil length	14.3 mm	13.9 mm	11.2 mm	12–20; 11–17 mm
Stamen length: Pistil length ratio	1.21	0.92	0.79	—
Ovules/pistil				
1986 (N = 30)	242.1	273.6	137.6	—
1988 (N = 30)	266.7	225.8	168.8	—
1995 (N = 25)	224.0	170.5	116.9	—
ave. (N = 85)	245.5	226.4	142.9	—
Pollen diam.	14.2 $\mu$ m	18.6 $\mu$ m	16.3 $\mu$ m	—
Somatic chromosome number	10	20	20	15; 30

<sup>1</sup> Character states, ranges, and averages based upon 30 plants of each species from the Kawayu area unless otherwise noted.

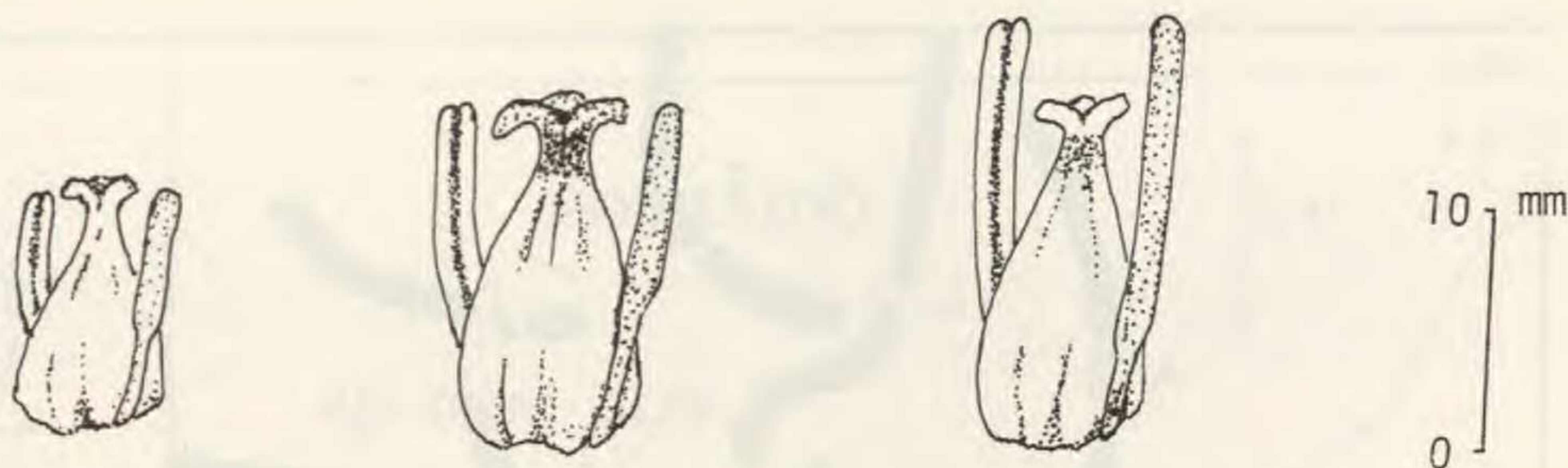
<sup>2</sup> Data derived from Samejima and Samejima (1962, 1987).

be *T. camschatcense* of Ker Gawler (1805) rather than *T. camtschaticum* Pallas ex Pursh (1814). The orthographic variant “*T. kamtschaticum*” has been the name most used for this species by recent authors. The binomial *T. camtschaticum* was cited by Pursh (1814) as a synonym of *T. obovatum*, a new species he proposed on the basis of specimens from Montreal, Canada. The Pallas specimens in the Lambert Herbarium (Pursh, 1814; Miller, 1970), which Pursh no doubt noted in 1811 (Stafleu & Cowan, 1983) as being labeled *T. camtschaticum* and collected in Kamtschatka, were not described by either Pallas or Pursh as a distinct taxon. Pursh clearly did not accept Pallas’s epithet for *T. obovatum*, and the specimens were not treated as something distinct. Rather, he stated, “The specimens in the herbarium of A.B. Lambert, Esq. agree in every respect with those from Canada.” We believe that this taxonomic opinion was incorrect and that *T. obovatum* is a taxonomic synonym of *T. grandiflorum* (Michaux) Salisbury, the accepted name for a species only distantly allied with Asiatic taxa

of *Trillium*. The name *T. camtschaticum* Pallas ex Pursh itself is simply a nomen nudum published pro syn., and Pursh’s primary intent apparently was to cite a collection he believed to represent the same species as his *T. obovatum*. As a nomen nudum *T. camtschaticum* lacks nomenclatural standing under both present and prior Codes, besides also being later than *T. camschatcense*.

We are indeed fortunate that the type collection of *T. camschatcense* mentioned by Ker Gawler (1805) as being in the Banksian Herbarium (now at BM) still exists; it comprises three sheets of specimens that bear a total of five stems, including three with good flowers. The holotype (labeled “TYPE SPECIMEN of *T. camschatcense* Ker-Gawl.”), the only stem that is not attached to a rhizome, is labeled “Kamtschatka ex herb. Dr. Pallas.” The other two sheets (isotypes) are labeled “TYPE COLLECTION of *T. camschatcense* Ker-Gawl.”: one isotype has two leaf-bearing stems from the same rhizome (with floral remnants only on one stem) and bears the handwritten label “*Trillium*





T. tschonoskii    T. channellii    T. camschatcense

Figure 2. Comparisons of pistils and stamens among *Trillium tschonoskii*, *T. channellii*, and *T. camschatcense*.

*camtschaticum*” at the top but no data concerning collector or locality; two flowering plants from separate rhizomes are mounted on the other (third) sheet, at the top of which are borne two “*T. camtschaticum*” labels in the same handwriting as the other isotype plus one that states “Herb. Pallas.” Various erroneous determinations provided via annotations to these specimens by later taxonomists (both unknown and well known) do not bear upon typification of *T. camschatcense*. This binomial is clearly based upon a collection by Pallas from Kamtschatka; any later species epithet based upon Pallas’s same collection (including the duplicate in Lambert’s herbarium cited by Pursh) must be treated as nomenclaturally synonymous even if other publication criteria were acceptable.

Early descriptions of *Trillium* species were so general as to fit almost any species, so the fact that *T. camtschaticum* came to be used for *Trillium* plants known to occur in eastern Russia (Kamtschatka) as well as Japan is not surprising. Publications on the Asian flora during the 19th Century (e.g., Ledebour, 1852; Miyabe, 1890) and early 20th Century (Makino, 1913) accepted *T. camtschaticum* or *T. obovatum* (more often as “*T. kamtschaticum*”) for any white-flowered *Trillium* or else called it *T. erectum* var. *japonicum* A. Gray (1858). Very few authors except Hultén (1927) have treated *T. camtschaticum* as invalid, but her publication of the new name *T. pallasii* failed to account for the earlier name by Ker Gawler also based upon Pallas’s collection. Now that four sexually fertile white-flowered species, including one diploid and three polyploids, are known for Japan alone, universal acceptance of *T. camschatcense* for the diploid is long overdue.

DISTINGUISHING CHARACTERISTICS OF *TRILLIUM*  
*CHANNELLII*

Some of the characteristics of *Trillium channellii* (Fig. 1) are intermediate between *T. camschatcense*

and *T. tschonoskii* as shown in Table 1. It expresses one morphological extreme in certain traits or more closely resembles one or the other of them in others. Leaf shape in *T. channellii* is more broadly elliptic than in either of the other two but is closer to *T. tschonoskii*. However, sepal and petal shapes and length:width ratios for these organs in *T. channellii* are much closer to *T. camschatcense*.

Other morphological features that distinguish these three species are those of the stamens and pistil. Comparative sketches of these floral parts are shown in Figure 2. In *Trillium camschatcense*, with long stamens, the ratio of stamen length to pistil length is ca. 1.2; in *T. tschonoskii*, with short stamens, this ratio is ca. 0.8; and in *T. channellii*, with stamens and pistils almost equal in length, the ratio is ca. 0.9. Both *T. channellii* and *T. camschatcense* show similar dark purple marks near the ovary apex, but these marks are lacking in *T. tschonoskii*. Ovules per pistil average about 245 for *T. camschatcense* and 226 for *T. channellii*, but in *T. tschonoskii* the average is much lower, only about 143.

Pollen fertility was determined for all three species in the Kawayu area to be higher than 94 percent, and pollen grains in *T. channellii* were found to be much larger than those of the other two species (Table 1). Since first observed in 1986, *T. channellii* has been the earliest of the three species to flower each year. Somatic chromosome number was determined from root tip squashes by the method of Darlington and LaCour (1938) to be  $2n$  ( $2x$ ) = 10 in *T. camschatcense* and  $2n$  ( $4x$ ) = 20 in both *T. channellii* (Fig. 3) and *T. tschonoskii* within the area of sympatry. From *T. hagai*, for which data are also shown in Table 1, *T. channellii* differs mainly by its tetraploid chromosome number and high degree of fertility. As a taxon present in both sterile triploid and fertile hexaploid forms in Japan, *T. ha-*



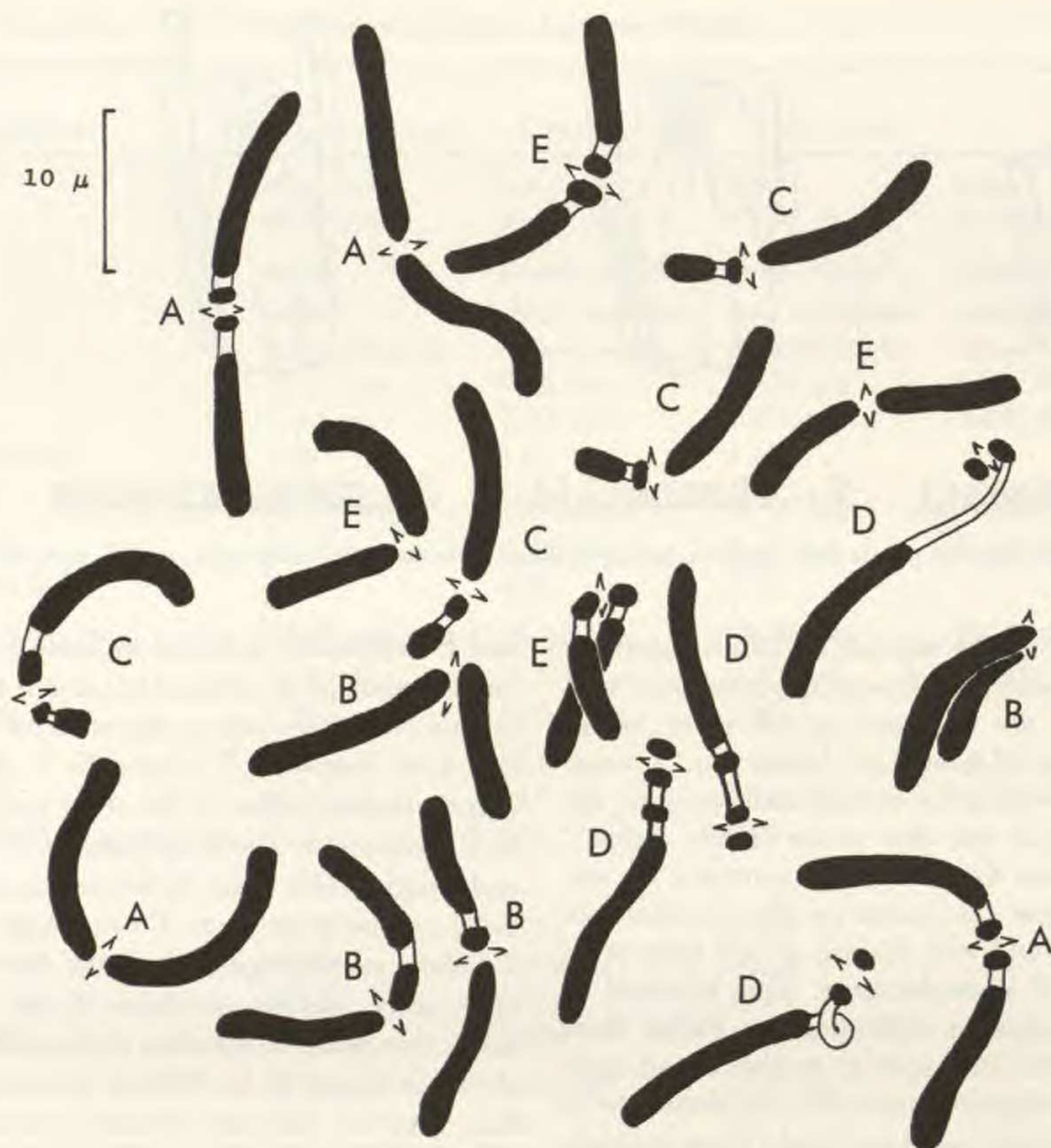


Figure 3. Chromosomes of *Trillium channellii* at mitotic metaphase showing differential staining patterns.

*gae* is intermediate between the parental taxa *T. camschatcense* and *T. tschonoskii* in most of its morphological features.

#### THE DISTRIBUTION AND HABITAT OF *TRILLIUM CHANNELLII*

The distribution of *Trillium channellii* (Fig. 4) is on the volcanic plain at the base of Mt. Yuo, especially in the Kawayu area along Kussharo Lake, Kawakami Co., Kushiro Dist., Hokkaido, Japan, where both *T. camschatcense* and *T. tschonoskii* also occur. Populations occur from near lakeside (254 m elev.) up to about 300 m elevation. Flowering specimens that were surveyed in a quadrat only 3 m × 10 m at the type locality (Fig. 5) were determined as follows: *T. channellii*, 51; *T. tschonoskii*, 14; and *T. camschatcense*, 10. In this area the first *Trillium* to reach anthesis (in late May) is *T. channellii*; several days later *T. tschonoskii* begins to flower; and *T. camschatcense* is last to flower after a few days more. When *T. camschatcense* and *T. tschonoskii* occur together to the south (Kushiro

Dist.), north (Abashiri Dist.), and east (Nemuro Dist.), the former species begins to flower several days to one week earlier than the latter. The reversal of the order that these species come into flower within the range of *T. channellii* could be linked to its origin in some way and may also reflect long-term local ecological effects of Mt. Yuo, now an active volcano, on nearby plant populations. We cannot prove this speculation on the basis of data now available, but we acknowledge such a possibility.

#### THE ORIGIN OF *TRILLIUM CHANNELLII*

At present we can offer two hypotheses concerning the origin of *Trillium channellii*, and each of them is supported by some (but not all) of the data available. Because both *T. camschatcense* and *T. tschonoskii* occur throughout the range of the new species and since all three share similar morphology, it was felt initially that *T. channellii* might be a hybrid between the two taxa with larger geographical ranges. As shown in Table 1, several of its



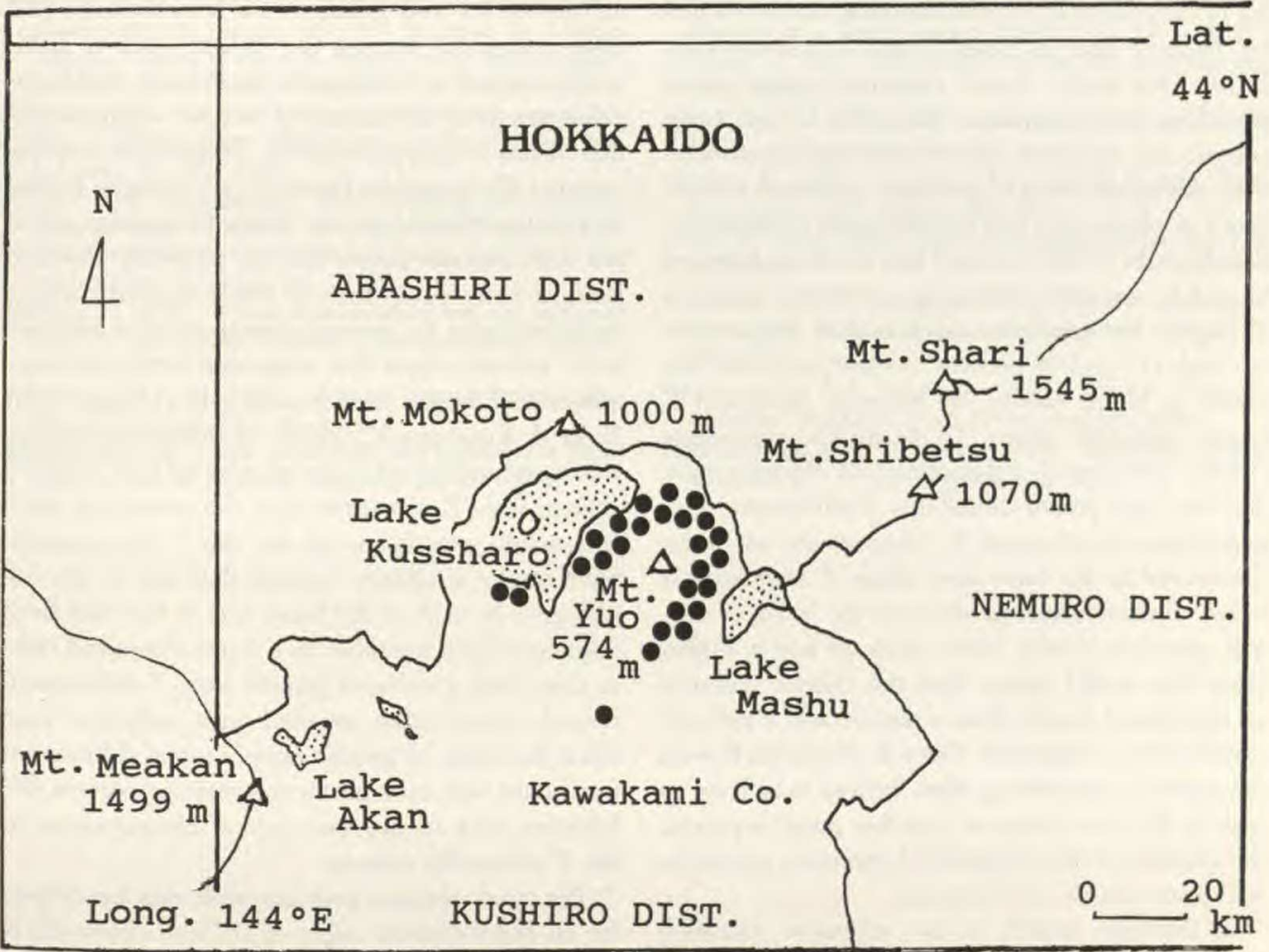


Figure 4. Distribution of *Trillium channellii* in eastern Hokkaido, Japan.

features are intermediate, and this at first led us to believe that these plants were *T. ×hagae*. Since *Trillium camschatcense* is diploid ( $2n = 10$ ) and *T. tschonoskii* tetraploid ( $2n = 20$ ), *T. channellii* could have originated from these putative parents only if the diploid contributed an unreduced gamete and *T. tschonoskii* a normal one. Combination of reduced and unreduced gametes is the most tenable explanation of triploid individuals occasionally found in North American *Trillium* taxa, all of which are diploid. Such an origin would give *T. channellii* the genomic constitution  $k_1k_1k_2t$  accord-

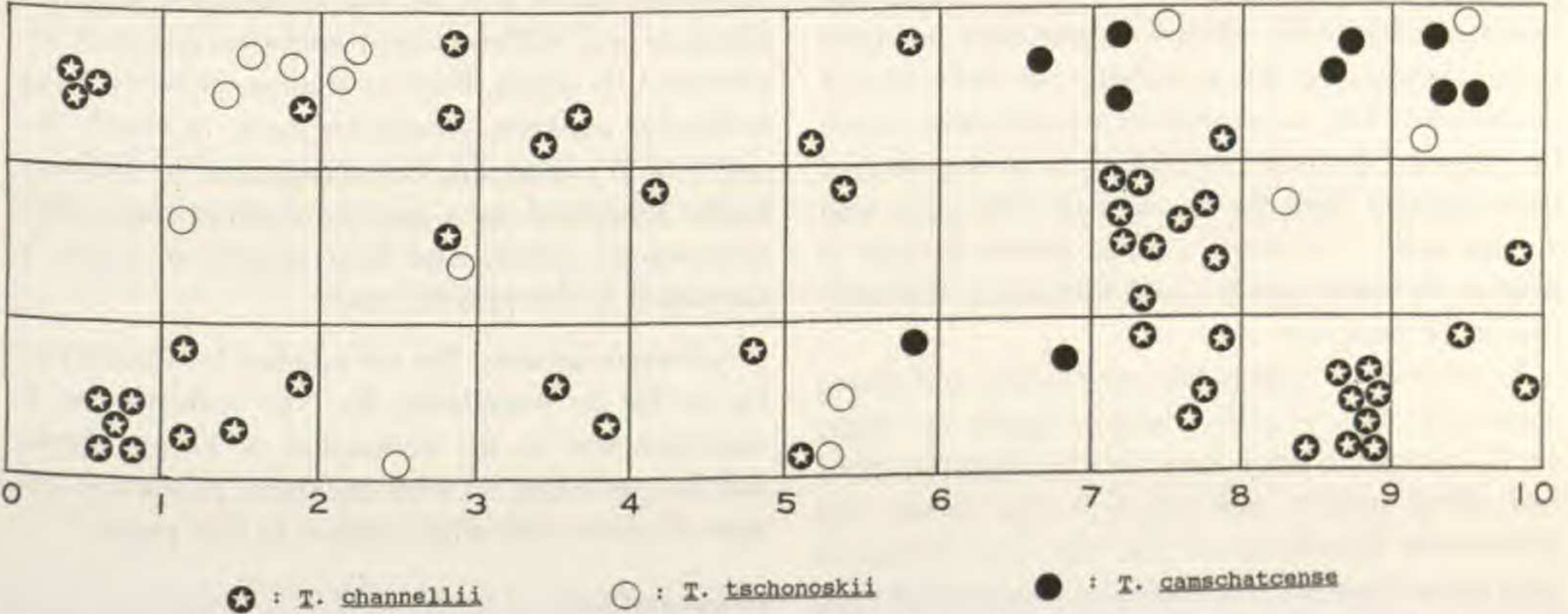


Figure 5. Quadrat (3 m  $\times$  10 m) showing locations of flowering plants of *Trillium channellii* and sympatric species at the type locality on 21 May 1994.



ing to the system of genome designations developed for *Trillium* taxa in Japan (Haga & Kurabayashi, 1953). One would expect numerous irregularities including both univalents (from the  $k_2$  and  $t$  genomes) and trivalents (from homeologous associations among all three of the basic genomes) at Meiosis I in plants with this chromosomal constitution. Kurabayashi (1958) reported that bivalents between  $k_2$  and  $k_1$  are rather common in triploid plants of *T. hagai*, but trivalent and univalent frequencies are high (12 and 86 percent, respectively), and the pollen is highly sterile. By contrast, hexaploid *T. hagai* regularly shows 15 bivalents, suggesting strictly homologous associations of chromosomes, and very high pollen stainability. Furthermore, triploid plants (i.e., typical *T. ×hagai*) are yet to be discovered in the same area where *T. channellii* is found. Such hybrids, products of the union of normal gametes, would likely form at much higher rates than would plants from the chance union of an unreduced gamete from a diploid and a reduced gamete from a tetraploid. Since *T. channellii* flowers the earliest, and since pollen fertility is at least as high in the new species as in either putative parent, the unreduced diploid gamete hypothesis cannot be accepted without equivocation.

A thorough search of the extensive literature concerning karyotypes of the Asiatic species of *Trillium* turned up no report of tetraploid plants that resemble *T. channellii* and *T. hagai* at sites where both *T. camschatcense* and hexaploid *T. hagai* are sympatric and form gametes with reduced chromosome numbers. If indeed the latter two species can hybridize, that hybrid would be a tetraploid with exactly the same genomes (i.e.,  $k_1k_1k_2t$ ) as one formed by union of an unreduced gamete from *T. camschatcense* and a reduced gamete from *T. tschonoskii*. *Trillium channellii* is so unlikely to have begun as a hybrid between hexaploid and diploid taxa, especially when *T. hagai* does not grow in the vicinity, that this possibility was not seriously considered. The same meiotic irregularities would be expected in such a tetraploid as in one derived from gametes from the two species that grow with *T. channellii*. As stated earlier, pollen fertility is high in the latter species, and this means that meiosis is very regular.

In addition to high pollen stainability in *Trillium channellii*, several other factors suggest an origin for *T. channellii* other than directly from the other two allied species with which it now occurs. An alternative hypothesis is that the new tetraploid may have originated by means of somatic doubling in a hybrid between *T. camschatcense* and a diploid taxon that is either now extinct or may exist only

as one of the two genomes in *T. tschonoskii*. All other polyploids among the Asiatic taxa of Trilliaceae (including *Trillium*, *Paris*, *Daiswa*, and *Kinugasa*) are generally accepted to have originated by this means of polyploidization. Differential staining patterns illustrated in Figure 3 (a karyotype typical of *T. channellii* plants) are identical for nine out of ten chromosome pairs. Having perfectly matched pairs of homologues for one whole diploid complement indicates far greater correspondence between basic genomes than that suggested for  $k_2$  and  $t$  genomes in *T. hagai* in previous studies (Haga, 1937; Haga & Kurabayashi, 1953). If these ten chromosomes are attributed to an unreduced (i.e., diploid) gamete from *T. camschatcense*, the remaining pairs still match exactly except for the C chromosome. Such strong similarity implies that one of the homologues in each of the basic sets of five may have originated from the other as a sister chromatid rather than from a reduced gamete from *T. tschonoskii*. Sexual reproduction coupled with sufficient time since its origin to permit chromosomal differentiation could well account for the staining pattern differences seen in just one pair of chromosomes in the *T. channellii* genome.

The most obvious problem with this hypothesis for an amphidiploid origin of *Trillium channellii* is the "missing" diploid parent. This stands as a real problem only if one maintains that the new species is of recent origin, and available data do not resolve that question. The geological period during which the  $k_2k_2$  and  $tt$  genomes in *T. tschonoskii* vanished from Japan (as diploids) is not known and may even have been the post-Pleistocene. Therefore, we suggest that *T. channellii* could be an allotetraploid of the genomic constitution  $k_1k_1tt$  or  $k_1k_1k_2k_2$ . The former genome combination appears more likely than the latter because high pollen stainability in *T. channellii* shows it to be well diploidized, and this points to well differentiated ancestral genomes involved in its origin. Further studies, possibly using molecular markers, should be made to clarify the origin of *T. channellii*, but recognition of this new fertile tetraploid as a species distinct from other autonomous species and their hybrids in Japan is warranted at the present time.

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